Catalogue of American Amphibians and Reptiles.

McCranie, J.R. 1993. *Crotalus durissus.*

Crotalus durissus Linnaeus
Neotropical Rattlesnake

Crotalus Durissus Linnaeus, 1758:214. Type-locality, "America," restricted to "Jalapa, Veracruz, Mexico" by Smith and Taylor (1950: 348), but not a good choice as the Veracruz population shows some differences from those of the other populations of this subspecies (see Klauber, 1952:60-61). Type-specimen originally in the Claudius Grill Suriname collection; later sent to the Zoölogiska Museet, Uppsala Universitet, Uppsala, Sweden, but now lost (Klauber, 1972:34). See Remarks (1).

Crotalophorus Durissus: Houttuyn, 1764:313.

Urocrotalon Durissus: Fitzinger, 1843:29.

Caudisona durissa: Cope, 1861:120. The first use of this combination that actually applied to this species.

Caudisona durissus: Sumichrast, 1881:270.

Crotalus devissus: Richardson, 1972:101. *Lapsus.*

Crotalus durrisus: Jacobson, 1986:167. *Lapsus*, not seen, *fide* Smith and Smith (1993:518).

• **Content.** Twelve subspecies are currently recognized: *durissus, cascavella, collilineatus, culminatus, cumanensis, dryinas, marajoensis, ruruima, terrificus, totonacus, trigonicus,* and *tzabcan.* See Remarks (2).

• **Definition and Diagnosis.** *Crotalus durissus* is a large species, with large adult males of some populations reaching about 1800 mm TL. However, several South American populations contain members that are stunted, with many adults not exceeding about 1000 mm TL. The species usually has a conspicuous vertebral ridge that is best developed in large adults, especially on the anterior portion of the body. Individuals from northeastern México tend to have a less-developed ridge. The dorsal ground color can be brown, reddish brown, grayish brown, yellowish brown, yellowish gray, yellowish olive, greenish gray, pale bluish gray, or nearly black. The body has 18-35 brownish or blackish diamond-shaped dorsal blotches, usually with lighter centers, except in many individuals from southern South America in which the center is not noticeably lighter than the rest of the blotch. The blotches are usually outlined by one row of paler colored scales. Posteriorly, the blotches tend to become shorter, wider, paler in color, somewhat obscure, and merge with the primary lateral blotches. The primary lateral blotches lie below the lateral points of the dorsal diamonds anteriorly. Paravertebral stripes that begin on the head posterior to and above the eyes usually extend about 1-4 head lengths onto the neck. The paravertebral stripes can be poorly defined in some specimens from northeastern México or may extend less than one head length onto the neck in animals from northeastern and central Brasil. Scutellation is as follows: 25-33 scale rows at midbody, all keeled except for the lowest 1-3 rows on each side; 159-196 ventrals in males, 165-195 in females (*C. unicolor*, if considered a subspecies of *durissus*, would lower the limits to 155 and 163, respectively); 22-34 subcaudals in males, 18-31 in females; 11-18 supralabials; 12-20 infralabials. The rostral usually is slightly higher than wide. The internasals and prefrontals are usually paired and in contact medially, although snakes from the Pacific versant of México northwest of the Isthmus of Tehuantepec tend to have the prefrontals subdivided into smaller scales, as do occasional specimens from throughout the species range. Anteriorly 2-5 (usually 2 or 3) intersupraoculars are present. The parietal and occipital regions are covered by small keeled scales, except in some specimens from northeastern México in which larger, irregular, vestigial parietals are present. The first supralabial usually is in broad contact with the prenasal, although a row of foveals may prevent this contact in specimens from southwestern México. Each side of the head has 1-8 loreals (usually 2 or 3, except in snakes from southwestern México, which usually have 4 or 5).

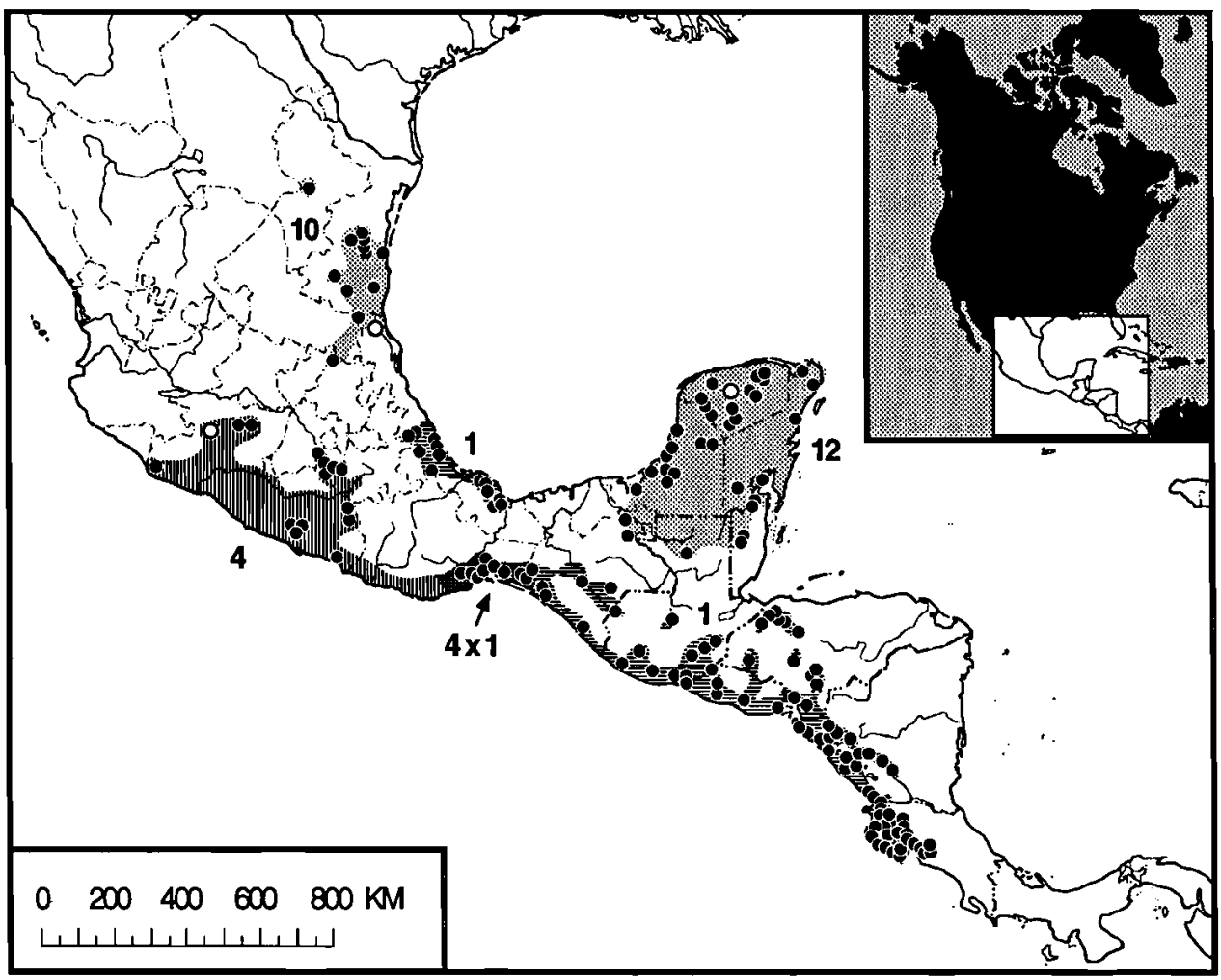
Crotalus durissus is the only species of rattlesnake occurring throughout much of its large geographical range. Only in México north of the Isthmus of Tehuantepec, in the savannas and alluvial plains of the southwestern portions of the Venezuelan states of Anzoátegui and Monagas, and on Aruba Island off the northern coast of South America does the range of *durissus* overlap or approach that of other species of *Crotalus* (but see Remarks [2] concerning the South American "species" *C. unicolor* and *C. vegrandis*). *Crotalus*

Figure. *Crotalus durissus totonacus* from pine-oak woodlands 5.6 km WSW El Lobo, Querétaro, México (photograph by L. Porras).

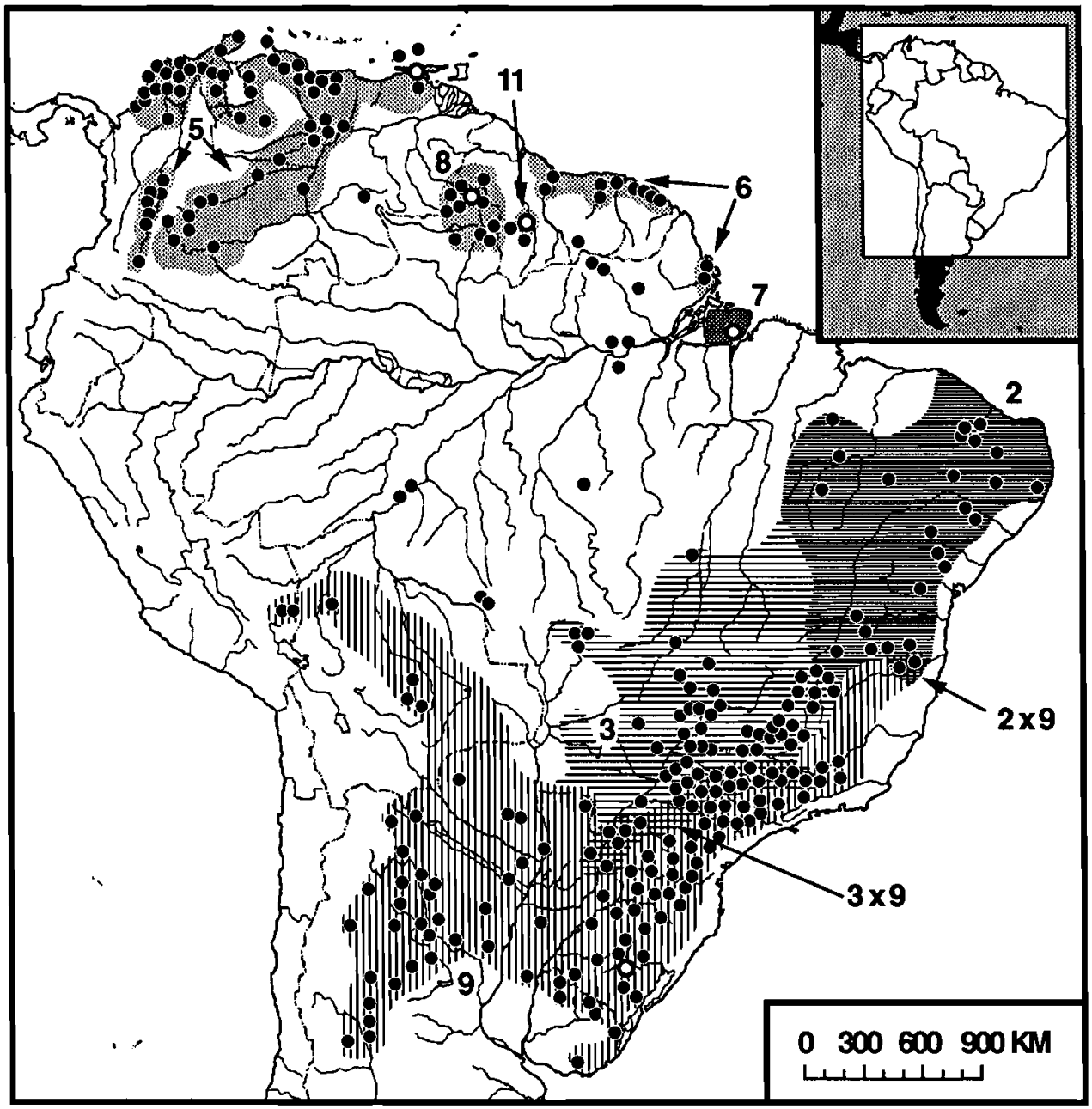
durissus approaches or overlaps the ranges of four large Mexican species (*atrox*, *basiliscus*, *molossus*, and *scutulatus*) north of the Isthmus of Tehuantepec. *Crotalus durissus* can be distinguished from each of these species by having conspicuous paravertebral stripes. *Crotalus durissus* can be further distinguished from *C. atrox* and *C. scutulatus* by having a strong vertebral ridge (no strong ridge), a nearly uniformly colored tail (strongly contrasting dark and pale rings), and usually having 4-6, except 4-10 on the Pacific versant, scales in the internasal-prefrontal area (usually 8 or more). *Crotalus durissus* can be further distinguished from *C. basiliscus* where their ranges overlap in southwestern Michoacán by having 27-33, usually 29, scale rows at midbody (24-29, or usually 27), 170-182 and 173-188 ventrals in males and females, respectively (178-201 and 184-206, respectively), and a nearly uniform tail color (gray with gray crossbands moderately evident). Typical *C. durissus* can be distinguished from *C. molossus* by having a distinct vertebral ridge, in addition to having paravertebral stripes. However, individuals of *durissus* in northeastern México, where the ranges of the two species overlap, resemble *C. molossus* in tending to loose the distinct vertebral ridge and in having poorly-defined paravertebral stripes (Fig. 1). Campbell and Lamar (1989) have suggested that these two species might hybridize in northeastern Querétaro. The northeastern Mexican population of *durissus* can usually be distinguished from *molossus* in having paired parietal and occipital stripes (absent or obscure and poorly-defined), a dark prefrontal crossbar (entire dorsum of head anterior to suboculars usually dark), and the primary lateral blotches lying below the lateral points of the dorsal diamonds anteriorly (dorsal blotches more often coalesced with the primary lateral series). South American *C. durissus* can be distinguished from *C. vegrandis* and *C. unicolor* by having well-defined dorsal diamonds and paravertebral neck stripes (diamonds and stripes obscured by numerous scattered white-tipped scales in *vegrandis* and diamonds and neck stripes faded and largely absent in adult *unicolor*).

• **Descriptions**. An excellent morphological and color description of *C. durissus* is in Campbell and Lamar (1989). Other good morphological and color descriptions are in Cei (1986), Gloyd (1940), Klauber (1952), Lancini and Kornacker (1989), Roze (1966), Vanzolini et al. (1980), and Wilson and Meyer (1985). Osteological features were described by Brattstrom (1964), and those of the hemipenis by Klauber (1972) and Vellard (1946).

• **Illustrations**. This is one of the most profusely illustrated species of all American amphibians and reptiles and the following citations are by no means exhaustive. Color illustrations of several subspecies are in Campbell and Lamar (1989), Hoge (1966), and Mehrtens (1987). Other good color illustrations are in Abuys (1987), Alvarez del Toro (1983), Amaral (1977), Bolaños (1984), Campbell and Brodie (1992), Carrizo (1988), Cei (1986), Chaves et al. (1990), Coborn (1991), Cruz (1987), Duvernoy (1836-1849), Freiberg (1982), Freiberg and Walls (1984), Gans (1975), Hoge and Romano-Hoge (1981a), Jahn (1983), Klemmer (1963), Kundert (1974, 1984), Lancini and Kornacker (1989), Levy (1983, as "Fer-de-lance"), Mercado (1975), Moonen et al. (1979), Obst et al. (1988), Pérez-Higareda and Smith (1991), Pérez-Santos and Moreno (1988), Perkins (1974), Roberts (1984), Rogé and Sauvanet (1987), Roze (1970), Schmidt (1990), Schmidt and Inger (1957), Schnitzler (1987), and Villa et al. (1988). Good black and white illustrations of several subspecies are in Glenn and Straight (1982), Gloyd (1940), Harris and Simmons (1972, 1978a), Hoge (1966), Hoge and Romano (1973), Hoge and Romano-Hoge (1981b), and Klauber (1956, 1972). Good black and white illustrations also occur in the following papers that are cited elsewhere in this account: Allen and Neill (1957), Amaral (1927b, 1977), Armstrong and Murphy (1979), Freiberg (1982), Gloyd and Kauffeld (1940), Harris and Simmons (1978b), Hoge and Romano-Hoge (1981a), Klauber



Map 1. The Mexican and Central American distribution of *Crotalus durissus*. Open circles mark type-localities, solid circles other records. The type-locality of the nominate subspecies is too imprecise to plot. Some solid circles may represent more than one locality.



Map 2. The South American distribution of *Crotalus durissus*. Open circles mark type-localities, solid circles other records. The type-localities of the subspecies *cascavella*, *collilineatus*, and *dryinas* are too imprecise to be plotted (the type-locality restriction for *cascavella* is invalid and that for *dryinas* is arbitrary). Some solid circles may represent several localities. The subspecific status of the many isolated Amazonian records is unknown. See McCranie (1984, 1986) for the ranges of *C. vegrandis* and *C. unicolor*, both of which are considered by some authors to be subspecies of *C. durissus*.

(1952), Lancini and Kornacker (1989), Roze (1966), Sage and Capredoni (1971), Sánchez-Herrera et al. (1981), Sandner Montilla (1975, 1980), Staněk (1962), and Tinoco (1978). Other illustrations and their subjects are: drawings of head scalation (Abalos et al., 1964; Campbell and Lamar, 1989; Cei, 1986; Chippaux, 1987; Glenn and Straight, 1982), osteological features (Brattstrom, 1964; Carrizo, 1988; Duvernoy,1836-1849; Roze, 1970; Ruiz, 1952; Tinoco, 1978), hemipenes (Prado, 1945; Roze, 1966; Vellard, 1946), karyotype (Beçak, 1966; Gutiérrez et al., 1979), microdermatoglyphic pattern (Arroyo and Cerdas, 1986; Hoge and Romano-Hoge, 1983; Picado, 1931; Stille, 1987), aberrant coloration (Abalos and Nader, 1967; Amaral, 1927a, 1927b, 1933a, 1934; Prado, 1945; Prado and Barros, 1941; Renault and Schreiber, 1951), bicephalic specimen (Amaral, 1927c; Belluomini, Biasi et al., 1978), heterologous copulation (Amaral, 1933b; Belluomini and Hoge, 1959).

• **Distribution.** In Middle America, *Crotalus durissus* occurs more-or-less continuously along the Pacific versant from southwestern and central Michoacán, México, to the western portion of the Meseta Central in west-central Costa Rica, with apparently continuous extensions into the Atlantic drainages of the Río Grijalva depression in Chiapas, México, and the middle and upper Río Motagua Valley in Guatemala. This species also occurs in several isolated populations on the Atlantic versant. In México, populations occur in west-central Nuevo León, from east-central Tamaulipas southward to extreme eastern Querétaro and northern Veracruz, in central Veracruz, and on the Peninsula de Yucatán from its outer edge to its base in northern Guatemala and Belize. In Guatemala, *C. durissus* is known from the upper Río Negro Valley, and in Honduras from the Sula Plain and the Comayagua Valley. Although no records of this species exist for Panamá, Clark (1942, 1952) reported seeing rattles from snakes from the dry tablelands around Tolé, Cañazas, and La Mesa in the provinces of Chiriquí and Veraguas (also see Lyman, 1949). Summary information on distribution and/or significant locality records for the Middle American countries are Belize (Henderson and Hoevers, 1975 [although these authors provide no documenta-

tion for their overstated range of this species in Belize, they do cite the few previously published records for the country], 1977), Costa Rica (Savage and Villa, 1986; Taylor, 1951; Taylor et al., 1974), El Salvador (Flores Villela et al., 1991; Mertens, 1952), Guatemala (Campbell and Vannini, 1989), Honduras (Cruz, 1987; Wilson and McCranie, 1991; Wilson and Meyer, 1985), México (Armstrong and Murphy, 1979; Camarillo, 1983; Gloyd, 1940; Johnson, 1989; Juliá Zertuche, 1981; Klauber, 1952; Lee, 1980; Pérez-Higareda and Smith, 1991; Powell and Parmerlee, 1980; Treviño, 1980), and Nicaragua (Villa, 1984).

In South America, the species occurs in all mainland countries except Chile and Ecuador (but see below) and on the Venezuelan islands of Margarita, Morro de la Iguana, and Tamarindo. *Crotalus unicolor*, considered a subspecies of *C. durissus* by some herpetologists, occurs on Aruba Island. In Colombia, *C. durissus* is known from the Río Magdalena Valley, the llanos north of the Río Guayabero/Guaviare, and in the Caribbean lowlands from the Departamento de Córdoba northeastward. In Venezuela, the species occurs throughout much of the northern and west-central portions, as well as in the Guiana highlands and a few isolated savannas in the southern part of the country. In the Guianas, a population occurs in the coastal lowlands from east-central Guyana to eastern French Guiana. Isolated populations also occur in west-central and southwestern Guyana. Northern Brazil has many isolated populations in Amapá, Pará, Roraima, Amazonas, and on Ilha de Marajó. In eastern Brazil, the species occurs more-or-less continuously from Ceará and Rio Grande do Norte southward to the borders of Paraguay, Argentina, and Uruguay, exclusive of the Atlantic coastal forests. In Bolivia, *C. durissus* occurs throughout most of the central portion of the country east of the Andes with an extension into the Río Madre de Dios drainage in southeastern Perú. In Paraguay, the species occurs throughout most of the country except for the extreme northeastern portion. In Argentina, the species occurs east of the Andes southward to southern Mendoza and San Luis provinces. In Uruguay, *C. durissus* occurs in the northern portion adjacent to Brazil and along the coast to the southeastern portion of the country in the Sierra de Minas near Solis de Mataojo. No actual records of *C. durissus* are known from Ecuador (Miyata, 1982; Peters, 1960), but the species may occur in southwestern Ecuador and adjacent Perú (Campbell and Lamar, 1989), as well as in the Departamento de Huánuco, Perú (Schmidt and Walker, 1943). Summary information on distribution and/or significant locality records for the South American countries are Argentina (Abalos et al., 1964; Cei, 1986; Freiberg, 1968; Sage and Capredoni, 1971), Bolivia (Gloyd, 1940), Brazil (Cunha and Nascimento, 1980, 1982; Gloyd, 1940; Hoge, 1966; Hoge and Romano-Hoge, 1981b; Jorge da Silva, 1993; Magalhães, 1958; Müller, 1968, 1973; Nascimento et al., 1988; O'Shea, 1990), Colombia (Müller, 1973; Pérez-Santos and Moreno, 1988; Renjifo, 1979), French Guiana (Chippaux, 1987; Hoogmoed, 1983), Guyana (Allen and Neill, 1957; Gloyd, 1940; Harris and Simmons, 1978b; Hoogmoed, 1983; Müller, 1968), Paraguay (Gallardo, 1979; Gatti, 1955; Gloyd, 1940; Scott and Lovett, 1975), Perú (Carrillo de Espinoza, 1983; Meneses, 1974; Schmidt and Walker, 1943), Suriname (Abuys, 1987; Hoge, 1964; Hoogmoed, 1983; Moonen et al., 1979), Uruguay (Achaval et al., 1978; Lema and Fabián-Beurmann, 1977; Orejas-Miranda, 1969), and Venezuela (Hoge, 1966; Lancini and Kornacker, 1989; Müller, 1968, 1973; Rivero Blanco and Dixon, 1979; Roze, 1966; Staton and Dixon, 1977).

Crotalus durissus is usually found in open, dry or semi-arid areas that have seasonal rainfall patterns. The species usually occurs below ~700 m elevation, but occasional populations may occur as high as 2200 m in Middle America and 2500 m in South America. Campbell and Lamar (1989) have discussed the vegetation types and altitudes where this species is found.

• **Fossil Record**. Langebartel (1953) recorded "*Crotalus* or *Bothrops*" vertebrae from early Holocene cave deposits in Yucatán, México.

• **Pertinent Literature**. Klauber (1972) presented much morphological and biological information on this species. Campbell and Lamar (1989), Smith and Smith (1976, 1993), and Villa et al. (1988) listed much literature on this species, and Armstrong and Murphy (1979) gave much information on the natural history of the species in México. Other works and their subjects are (with few exceptions, literature prior to 1970 is not cited here as it is usually cited in the papers mentioned): ecological notes within a snake community, Henderson and Hoevers (1977), Vitt and Vangilder (1983); suggested mimicry, Sánchez-Herrera et al. (1981); behavioral notes in captivity, Chiszar, Wellborn et al. (1980), Cordeiro et al. (1981), Hoge et al. (1981), Wellborn et al. (1982); longevity in captivity, Snider and Bowler (1992); feeding mechanism, Kardong et al. (1986); strike-induced chemosensory searching, Chiszar et al. (1978, 1982, 1988), Chiszar, Duvall et al. (1980), Duvall et al. (1980), Radcliffe et al. (1980), Scudder et al. (1983); literature review on combat rituals, Carpenter (1986); reproduction, Araujo and Perazzolo (1974), Dundee et al. (1986), Fitch (1985), Gonçalves (1971), Langlada (1973), Langlada et al. (1974), Peterson (1983), Solórzano and Cerdas (1988); birth defects, Langlada (1974); literature review on axial bifurcation, Smith and Pérez-Higareda (1987); aberrant coloration, Hoge (1953), Villa (1984), also see Illustrations; parasites and/or diseases, Baker (1987) and Murphy and Armstrong (1978) reviewed much of the literature, papers not cited by them are Arroyo et al. (1980), Belluoimini, Saliba, and Abe (1978), Biasi et al. (1973, 1976, 1981), Furlanetto et al. (1979), Johnson (1982), Machado (1966), Moreno and Bolaños (1977), Pessôa and Biasi (1974), Pessôa et al. (1974), Quintero et al. (1990), Rego (1983a, 1983b, 1983c), Santa Rosa et al. (1980); cytological and/or molecular studies, Beçak (1966, 1968), Cadle (1992), Gutiérrez et al. (1979), Minton (1992), Olmo (1984, 1986), Prezoto et al. (1991), Rodrigues and De Lucca (1973, 1974), Schreiber et al. (1967), Sullivan (1974), Werman (1992); microdermatoglyphics, Arroyo and Cerdas (1986), Stille (1987); cranial myology, Groombridge (1986), Haas (1973), Kardong et al. (1986); vertebral meaurements, Christman (1975); sexual size differences, Fitch (1981); role in Mayan culture, Diaz-Bolio (1988); head glands, Kochva (1978), Langlada et al. (1973), Lopes et al. (1972, 1975); pit organ, Barrett (1970); urinogenital system, Fox (1977); lymphoid aggregation, Langlada et al. (1981); fine structure of liver cells, Alemán (1972); coronary arteries, Erhart (1935); pulmonary artery, Brongersma (1951); surgical techniques, Langlada and Belluomini (1973a, 1973b), Langlada and Shinoiya (1973), Oliveira et al. (1988). A voluminous amount of literature is available on the venom and snake-bite of this species. A good introduction to the literature on the venom can be found in Elliott (1978), Mebs (1978), and the various chapters in Tu (1982) and that on snake-bite can be found in Hardy (1989) and Watt (1989).

• **Remarks**. (1) Linnaeus (1758) proposed the names *horridus*, *durissus*, and *dryinas* for three species of rattlesnakes. The former two names were variously applied by early workers to the Neotropical Rattlesnake and to the two North American species known today as *C. horridus* and *C. adamanteus* (see the synonymies for the respective species in Gloyd, 1940). Klauber (1941) provided a detailed analysis of the data and references provided by Linnaeus (1758) and concluded that the name *durissus* was best applied to the Central American populations of the Neotropical Rattlesnake, a conclusion also reached by Gloyd (1940). Gloyd (1940) and Klauber (1941) also pointed out that the South American populations that were being called *Crotalus terrificus* (Laurenti, 1768) were conspecific with the Central American populations. Unfortunately, some South American workers have continued to use *terrificus* as the specific name for this rattlesnake. Recently, Sandner Montilla (1975, 1983) even presented weak discussions trying to suppress the name *durissus* in favor of *terrificus*.

(2) The South American subspecies of *C. durissus* are poorly defined and often difficult to distinguish. A thorough systematic study of these populations, along with those occurring in Middle America, is needed and was suggested by McCranie and Wilson (1979) and Wilson and Meyer (1985). The scalation data included in the subspecies definitions were taken from the literature. As a result, the ventral, subcaudal, and scale rows at midbody ranges given are considered deficient for many subspecies, especially those occurring in South America. Campbell and Lamar (1989) considered *Crotalus vegrandis* Klauber and *C. unicolor* Van Lidth de Jeude to be subspecies of *C. durissus*. These were previously treated in the Catalogue of American Amphibians and Reptiles as species separate from *durissus* by McCranie (1984, 1986). Subsequent publications on these two taxa are as follows: *unicolor* (color photos: Campbell and Lamar, 1989; Mehrtens, 1987; habitat photograph: Goode et al., 1990; fertility: Loomis and Smith, 1987; microdermatoglyphics: Stille, 1987; species survival plan: Tryon, 1986; strike-induced chemosensory searching: Chiszar et al., 1992; Goode et al., 1990; studbook: Olney et al., 1988; viral diseases: Smith et al., 1986), *vegrandis* (captive reproduction: Muir, 1984; color photos: Campbell and Lamar, 1989; Coborn, 1991; Kundert, 1984; Lancini and Kornacker, 1989; Mehrtens, 1987; Tashjian, 1991; Trutnau, 1982; male courtship on a strike-induced chemosensory searching female: Chiszar et al., 1984; microdermatoglyphics: Stille, 1987; venom: Kaiser and Aird, 1987).

Frost and Hillis (1990) suggested that *Crotalus durissus* may be composed of several evolutionary species.

(3) *Crotalus pifanorum* was described by Sandner Montilla (1980) on the basis of one, apparently adult, female specimen. The specimen was reported to be only 652 mm TL. Other than its apparent small size, the specimen falls within the range of variation reported for *C. d. cumanensis* and is tentatively included herein in the synonymy of that subspecies, as was suggested also by Campbell and Lamar (1989).

(4) *Crotalus durissus neoleonensis* Juliá Zertuche, *in* Harris and Simmons (1978a) is a *nomen nudum*, as no diagnostic characteristics were stated nor was a holotype designated. Treviño (1978) provided data from the three specimens upon which the name was based (the number of ventrals given for one specimen is so low as to suggest a typographical error). From these data, this population appears very similar to *C. d. totonacus*.

(5) *Crotalus durissus trigonicus* Harris and Simmons probably is not distinct from *C. d. ruruima*, as variation within the few known specimens of *trigonicus* appears to be encompassed by that known for *ruruima*. Abuys (1987), Cunha and Nascimento (1980), and O'Shea (1990) have also expressed some doubt as to the validity of this taxon. In addition, problems associated with the holotype selection and the diagnosis provided by Harris and Simmons (1978b) are discussed by McCranie and Wilson (1979).

• **Etymology.** The name *durissus* (L., *durus* = hard or tough; L., *-issimus* = very) probably refers to the sturdy dorsal scales and ridge in this species; *cascavella* is from the Portuguese word *cascavel*, meaning rattle; *collilineatus* (L., *collum* = neck; L., *linea* = a line; L., *-atus* = provided with) refers to the paravertebral and paraventral stripes on the neck; *culminatus* (L., *culmen* = a ridge; L., *-atus* = provided with) refers to the strong vertebral ridge; *dryinas* is probably derrived from the Greek word *dryas* = a wood or tree-nymph, the meaning of which is unclear; *marajoensis* is named for Ilha de Marajo; *ruruima* is the local Indian name for Mount Roraima; *terrificus* (L., *terrificus* = dreadful or frightful) apparently refers to the fear invoked in humans by this snake; *totonacus* is named after the Totonacs, an ancient Indian tribe of Veracruz, México; *trigonicus* (Gr., *trigonos* = triangular; L., *-icus* = belonging to) apparently in reference to "V shaped" markings on the supraoculars; *tzabcan* was said by the describer to be a Mayan word for rattlesnake.

1. *Crotalus durissus durissus* Linnaeus

Crotalus Durissus Linnaeus, 1758:214 (see species synonymy).
Crotalus simus Latreille, *in* Sonnini and Latreille, 1801:202. Type-locality, "Ceylan [in error]." No holotype designated, based on Plate 45, fig. 4 in Seba (1735); also see Thireau (1991:4).
Crotalus terrificus durissus: Amaral, 1929:5 (part).
Crotalus durissus durissus: Klauber, 1936:4 (part).
C[rotalus]. terrificus copeanus Amaral, 1937:162. Type-locality, "America Central." No holotype designated. Intended as a substitute name for *Crotalus durissus durissus*.
Crotalus durisus durisus: Smith and Smith, 1993:518. *Lapsus*, originally used in Avila Soriano (1987:22), a dissertation.

• **Definition.** Paravertebral stripes on neck extend more than one head length (1-4, usually 2-2 1/2), comprising 2-3 contiguous scale rows (paravertebral stripes can be lacking in some large adults), usually without conspicuously lighter centers; usually no paraventral stripes on neck; dorsal diamonds with somewhat lighter centers. Ventrals number 161-184 in males, 172-187 in females; subcaudals 28-34 in males, 20-27 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-31 (usually 29, less frequently 27). This subspecies is large, reaching at least 1800 mm TL. See Remarks (2).

2. *Crotalus durissus cascavella* Wagler

Crotalus cascavella Wagler, 1824:60. Type-locality, "in campis provinciae Bahiae." Hoge (1966:139) restricted the type locality to "Mina Caraiba, Bahia [Brasil]" by neotype selection (Instituto Butantan Herpetologia 23400), but Hoge's neotype selection is invalid (see Hoogmoed and Gruber, 1983).
Crotalus terrificus var. *collirbombeatus* Amaral, 1927b: 90. Type-locality, "zona N. E. do Brasil." No holotype designated.
C[rotalus]. durissus cascavella: Klauber, 1956:32 (as a possibly valid form). Hoge (1966:139) formally recognized the subspecies without providing any diagnostic characteristics.
Crotalus durissus cascarella: Roberts, 1984:56. *Lapsus.*

• **Definition.** Paravertebral stripes on neck extend less than one head length, comprising 2-3 contiguous scale rows, without distinctly lighter centers; short paraventral stripes are usually present on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 167-175 in males, 172-180 in females; subcaudals 28-29 in males, 22-31 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-29 (usually 27 or 29). This subspecies is large, reaching at least 1600 mm TL.

3. *Crotalus durissus collilineatus* Amaral

Crotalus terrificus var. *collilineatus* Amaral, 1927b:90 (part). Type-locality, "zonas do Centro, S. E. e S.do Brasil e bem assim da Argentina, Paraguay e provavelmente Uruguay e Bolivia," restricted to "State Mato Grosso [Brasil]" by lectotype selection (Hoge, 1966:139). Lectotype, Instituto Butantan Herpetologia 2180, sex, date, and collector not given (Hoge, 1966:139) (not examined by author).
Crotalus terrificus crotaminicus Gonçalves, 1956:367. Type-locality, "da região de Morro Agudo, Franca e Ituverava [State of São Paulo, Brasil]." No holotype designated. *Nomen nudum*, because the description does not comply with the rules of the International Commision on Zoological Nomenclature.
Crotalus durissus collilineatus: Hoge, 1966:139.
C[rotalus]. d[urissus]. collelineatus: Langlada et al., 1974:253. *Lapsus.*
Crotalus durissus collineatus: Mercado, 1975:28. *Lapsus.*

• **Definition.** Paravertebral stripes on neck extend more than one head length, comprising 2-3 contiguous scale rows, usually without distinctly lighter centers; short paraventral stripes and accessory blotches are usually present on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 168-175 in males, 177-184 in females; subcaudals 27-31 in males, 21-23 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-31 (usually 27 or 29). This subspecies is large, reaching at least 1600 mm TL.

4. *Crotalus durissus culminatus* Klauber

Crotalus durissus culminatus Klauber, 1952:65. Type-locality, "El Sabino near Uruapan, Michoacán, Mexico." Holotype, Field Museum Natural History 126616 (formerly Edward H. Taylor 5224), a juvenile female collected by E.H. Taylor and H.M. Smith in 1936 (not examined by author).

• **Definition.** Paravertebral stripes on neck extend more than one head length (1-3, usually about 2), comprising a single scale row throughout more than half of their lengths and in 2 contiguous scale rows in remainder of length, without distinctly lighter centers; usually no paraventral stripes on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 170-182 in males, 173-188 in females; subcaudals 25-32 in males, 20-28 in females. Usually more than 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 27-33 (usually 29, less frequently 31). This subspecies is large, reaching at least 1355 mm TL.

5. *Crotalus durissus cumanensis* Humboldt

Crotalus cumanensis Humboldt, 1813:6. Type-locality, "Cumana [Venezuela]." No holotype designated.
Crotalus Loeflingii Humboldt, 1813:6. Type-locality, "Cumana [Venezuela]." No holotype designated.
Caudisona Loeflingii: Cope, 1861:120.
C[rotalus]. durissus cumanensis: Klauber, 1956:32 (as a possibly valid form). Hoge (1966:142) formally recognized the subspecies and gave a definition of its purported range, but without providing any diagnostic characteristics.
Crotalus durissus cumanensis: Hoge,1967:223. *Lapsus.*
Crotalus terrificus cumanensis: Sandner Montilla, 1975:51.
Crotalus pifanorum Sandner Montilla, 1980:2. Type-locality, "sesenta y ocho kilómetros al S. de la población de Espino, en dirección de Puerto Parmana, Parcelamiento de Agrotécnicos 'Dr. Gonzalo Ledezma', entre los nacientes de los rios Otocuao (Este) y Carapa (Oeste), Distrito Infante, Estado Guárico [Venezuela]." Holotype, Serpentario del Instituto Venezolano de Ofidi-

ología Cp No. 1, an adult female, collected by Hernán Rauseo M, in "a mediados" of 1980. See Remarks (3).
Crotalus durissus cuminamensis: Bücherl, 1980:122. *Lapsus.*
C[rotalus]. d[urissus]. pifanorum: Péfaur, 1992:15.

• **Definition.** Paravertebral stripes on neck extend more than one head length, comprising 2-3 contiguous scale rows, without distinctly lighter centers; paraventral stripes on neck long or consisting of many shorter broken stripes and usually more than one scale row wide; dorsal diamonds with distinctly lighter centers. Ventrals number 161-188 in males, 165-188 in females; subcaudals 22-34 in males, 20-32 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-31 (usually 27 or 29). This subspecies is large, reaching at least 1750 mm TL.

6. *Crotalus durissus dryinas* Linnaeus

Crotalus Dryinas Linnaeus, 1758:214. Type-locality, "America," restricted to "Paramaribo, Surinam" by Hoge (1966:143). Type-specimen originally in the Museum Adolphi Friderici; later sent to the Zoölogiska Museet, Uppsala Universitet, Uppsala, Sweden, but now lost (Klauber, 1972:35).
Crotalophorus Dryinas: Houttuyn, 1764:310.
Caudisona Dryinas: Laurenti, 1768:94.
Crotalus strepitans Var. *dryinas:* Daudin, 1803:320.
Crotalus durissus dryinus: Hoge, 1966:142. *Lapsus.*
Crotalus durissus dryinas: Klauber, 1972:35.

• **Definition.** Paravertebral stripes on neck extend more than one head length, usually one scale row wide, without distinctly lighter centers; paraventral stripes on neck nearly continuous and one scale row wide; dorsal diamonds with distinctly lighter centers. Ventrals number 164-175 in males, 171-177 in females; subcaudals 24-32 in males, 23-24 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 27-31. This subspecies is large, reaching at least 1500 mm TL.

7. *Crotalus durissus marajoensis* Hoge

Crotalus durissus marajoensis Hoge, 1966:143. Type-locality, "Tuiuiu, Ilha de Marajó, State Pará, Brasil." Holotype, Instituto Butantan Herpetologia 17779, an adult female collected by A.R. Hoge, date not given (not examined by author).

• **Definition.** Paravertebral stripes on neck extend more than one head length, comprising 2-3 contiguous scale rows, without distinctly lighter centers; no paraventral stripes on neck (only a series of scattered black scales); dorsal diamonds with distinctly lighter centers. Ventrals number 159-168 in males, 165-174 in females; subcaudals 25-30 in males, 20-22 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 27-31 (usually 27 or 29). This subspecies is large, reaching at least 1500 mm TL.

8. *Crotalus durissus ruruima* Hoge

Crotalus durissus ruruima Hoge, 1966:145. Type-locality, "Paulo Camp, 4000 ft., at Venezuelan versant of Mount Roraima, Venezuela." Holotype, American Museum Natural History 36056, an adult female collected by the Tate expedition in 1927 (not examined by author).
Crotalus terrificus ruruima: Sandner Montilla, 1980:7.
Crotalus durissus rurima: Harding and Welch, 1980:66. *Lapsus.*

• **Definition.** Paravertebral stripes on neck extend more than one head length, usually comprising 3-4 contiguous scale rows, with distinctly lighter centers; paraventral stripes or a series of dashes usually present on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 167-172 in males, 174-177 in females; subcaudals 25-32 in males, 21-23 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 27-29. Many specimens of this subspecies are stunted and <1000 mm TL, though some specimens do exceed 1500 mm TL.

9. *Crotalus durissus terrificus* (Laurenti)

Caudisona terrifica Laurenti, 1768:93. Type-locality, "America infra gradum elev. 45," restricted to "Julio de Castilho, Município Taquari, State Rio Grande do Sul, Brasil" by neotype selection (Hoge, 1966:147). Neotype, Instituto Butantan Herpetologia 22997, an adult female, collector and date not given (Hoge, 1966:147) (not examined by author).
Crotalus exalbidus Boddaert, 1783:16. Type-locality not given. No holotype designated.
Crotalus immaculatus Latreille, *in* Sonnini and Latreille, 1802:201. Type-locality, "Indes orientales [in error]." No holotype designated, based on Plate 95, fig. 3 and Plate 96, fig. 1 in Seba (1735), both plates reproduced by Aramata (1990:258 [the patternless snake] and 259, respectively); also see Thireau (1991:2-3).
Crotalus strepitans Daudin, 1803:318. Type-locality, "l'Amérique." No holotype designated, based on Plate 95, fig. 3 and Plate 96, fig. 1 in Seba (1735), both plates reproduced by Aramata (1990: 258 [the patternless snake] and 259, respectively); also see Thireau (1991:4).
C[rotalus]. terrificus: Cope, *in* Yarrow, 1875:532 (part).
[*Crotalus terrificus* var. *terrificus*]: Amaral, 1927b:90. By inference.
Crotalus terrificus var. *collilineatus* Amaral, 1927b:90 (part). See *collilineatus* subspecies account.
Paracrotalus terrificus: Reuss, 1930:88.
Crotalus durissus terrificus: Klauber, 1936:4 (part).
Crotalus durissimus terrificus: Staněk, 1962:63. *Lapsus.*

• **Definition.** Paravertebral stripes on neck extend more than one head length (usually at least three head lengths), usually comprising 2 contiguous scale rows (paravertebral stripes can be indistinct in some adults), without distinctly lighter centers; long paraventral stripes on neck (paraventral stripes can be indistinct in some adults); dorsal diamonds without distinctly lighter centers. Ventrals number 161-179 in males, 171-190 in females; subcaudals 27-32 in males, 19-25 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-33 (usually 27 or 29). This subspecies is large, reaching at least 1500 mm TL.

10. *Crotalus durissus totonacus* Gloyd and Kauffeld

Crotalus totonacus Gloyd and Kauffeld, 1940:12. Type-locality, "Panaco Island, about 75 miles south of Tampico, Veracruz, 12 miles inland from Cabo Rojo." Holotype, Chicago Academy Sciences 4469, a subadult female collected by Willis Woolems in May 1933 (not examined by author).
Crotalus durissus totonacus: Smith and Taylor, 1945:190.
Crotalus basiliscus totonacus: Taylor, 1950:453.
Crotalus durissus totonocus: Tu, 1971:91. *Lapsus.*
Crotalus durissus neoleonensis Juliá-Zertuche, *in* Harris and Simmons, 1978a:111. *Nomen nudem.* See Remarks (4).
C[rotalus]. durissus totonacis: Gopalakrishnakone et al., 1979:57. *Lapsus.*

• **Definition.** Paravertebral stripes on neck usually poorly defined, with irregular borders; usually no paraventral stripes on neck; dorsal diamonds with somewhat lighter centers. Ventrals number 187-196 in males, 189-195 in females; subcaudals 24-29 in males, 22-26 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 25-27. This subspecies is large, reaching at least 1800 mm TL.

11. *Crotalus durissus trigonicus* Harris and Simmons

Crotalus durissus trigonicus Harris and Simmons, 1978a:112. *Nomen nudum.*
Crotalus durissus trigonicus Harris and Simmons, 1978b:305. Type-locality, "Rupununi Savanna of southwestern Guyana." Holotype, Natural History Society of Maryland RS 907 HSH/RSS, an adult female, collector not given, collected in December 1970 (not examined by author). See Remarks (5).

• **Definition.** Paravertebral stripes on neck extend more than one head length, usually comprising 2 contiguous scale rows, without distinctly lighter centers; paraventral stripes or a series of dashes usually present on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 170-172 in males, 177-178 in females; subcaudals 29-31 in males, 21-23 in females. Usually 4 scales are

present in the internasal-prefrontal area. Scale rows at midbody number 29-31. This subspecies is stunted, reaching about 1150 mm TL.

12. *Crotalus durissus tzabcan* Klauber

Crotalus durissus tzabcan Klauber, 1952:71. Type-locality, "Kantunil, Yucatán, Mexico." Holotype, Field Museum Natural History 36168, a young male collected by E. Wyllys Andrews on 28 October 1939 (not examined by author).

Crotalus durisus tzabcan: Maruska, 1979:21. *Lapsus*, not seen, *fide* Smith and Smith (1993:518).

• **Definition.** Paravertebral stripes on neck extend from 1 - 2 1/2 (average about 1 1/2) head lengths, comprising 1-3 (2 predominating, narrowing posteriorly) contiguous scale rows, without distinctly lighter centers; no paraventral stripes or spots on neck; dorsal diamonds with distinctly lighter centers. Ventrals number 177-188 in males, 182-191 in females; subcaudals 25-33 in males, 23-27 in females. Usually 4 scales are present in the internasal-prefrontal area. Scale rows at midbody number 27-29 (more frequently 29). This subspecies is large, reaching at least 1750 mm TL.

• **Acknowledgments.** I thank K. Adler, R.W. McDiarmid, J.E. Simmons, and H.M. Smith for their help in obtaining copies of several publications. Adler also provided information on Seba's rattlesnake plates.

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Primary editor for this account, Larry David Wilson.

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